

Estimating occupancy using spatially and temporally replicated snow surveys

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Abstract

Occupancy modelling is increasingly used to monitor changes in the spatial distribution of rare and threatened species. Occupancy methods have traditionally relied upon temporally replicated surveys to estimate detection probability. Recently, occupancy models with spatial replication have been used to estimate detection probabilities over large geographical areas that are difficult to survey repeatedly. We developed occupancy models that combine spatially and temporally replicated data and applied them to snow-tracking surveys of six species, including wolverine *Gulo gulo* and Canadian lynx *Lynx canadensis*. We surveyed thirty-nine 100-km² cells and used 1-km trail segments within cells as spatial replicates. We surveyed 56% of the cells once and 44% of the cells between 2 and 14 times, resulting in a total of 872 km surveyed. We compared four occupancy models that incorporated spatial correlation in detection probability and hierarchically estimated occupancy at two spatial scales: cell occupancy and segment presence. We detected strong serial correlation in probability of detection for all species. Our models with serial correlation had higher occupancy estimates with larger confidence intervals than models assuming segments were independent and exchangeable. Spatial and temporal replicates have identical power to detect decreases in occupancy when survey segments are independent, but spatial correlation in detection probability can reduce the power of spatial replicates. The effects of spatial correlation are more pronounced when detection probability is low. Application of temporal replicates to spatial replicated surveys increases the precision of occupancy estimates, but sampling design trade-offs between number of sites and spatial versus temporal replicates need to balance levels of spatial correlation in detection probability with costs to visit sites.

Introduction

Occupancy modelling has increasingly been used throughout the world to monitor changes in species distribution (MacKenzie *et al.*, 2002, 2006). Occupancy modelling methods can account for imperfect detection, whereby the species was present but not detected. These methods provide both estimates of occupancy and probability of detection. Detection probabilities are traditionally estimated from temporally replicated surveys or multiple observers (MacKenzie *et al.*, 2006). Temporal survey replicates can be expensive and logistically difficult to implement in some study areas. An alternative method for estimating detection probabilities is to use randomly selected spatial replicates with replacement (MacKenzie *et al.*, 2006). However, random sampling with replacement can be inefficient, and Guillera-Arroita (2011) found that sampling without

replacement does not induce bias in the occupancy estimator as long as the probability of species presence on one replicate is not influenced by species presence on other replicates within the same cell. Hines *et al.* (2010) addressed spatial correlation among adjacent segments on linear transects by modelling serial correlation in detection probability or probability of presence as Markovian processes. Spatially replicated occupancy surveys have primarily been applied to track surveys covering large geographical areas for wide-ranging species such as tigers *Panthera tigris* on trails in India (Hines *et al.*, 2010), tigers on transects in Sumatra (Wibisono *et al.*, 2011) and brown hyenas *Hyaena brunnea* on roads in Africa (Thorn *et al.*, 2011). For both temporally and spatially replicated study designs, increasing the number of replicates increases the cumulative probability of detecting the species at least once and improves precision for estimates of detection probability and occupancy.

Thus, combining temporal and spatial replication could improve occupancy estimates for rare species occurring in expansive study areas that are difficult to survey. Hierarchical occupancy models combining spatial and temporal replicates have received scant attention (Nichols *et al.*, 2008; Mordecai *et al.*, 2011; Pavlacky *et al.*, 2012; see review by Bailey, MacKenzie & Nichols, 2013) and have not been applied to long, linear track surveys.

Snow-tracking surveys have been used extensively to estimate species distribution and relative abundance using both ground (Thompson *et al.*, 1989; Stanley & Bart, 1991; Hayward *et al.*, 2002; Stephens *et al.*, 2006; Linnell *et al.*, 2007) and aerial-based surveys (Becker, Spindler & Osborne, 1998; Golden *et al.*, 2007; Magoun *et al.*, 2007; Gardner *et al.*, 2010; Aing *et al.*, 2011; Webb & Merrill, 2012). Aerial surveys usually focus upon single species within open landscapes, whereas ground surveys detect multiple species within both open and forested landscapes. Snow conditions and animal movement rates on these surveys universally influence track detection. A variety of approaches have been used to address the effects of movement rates and snow conditions on survey results. These approaches include simply selecting ideal survey conditions to maximize detection probability (Thompson *et al.*, 1989; Becker *et al.*, 1998), including sampling time and distance as explanatory variables affecting track counts (Hayward *et al.*, 2002; Stephens *et al.*, 2006), and estimating detection rates through simulation of animal movements and survey intensity (Stephens *et al.*, 2006; Linnell *et al.*, 2007; Webb & Merrill, 2012). More recently, occupancy modelling approaches have been used for aerial snow-tracking surveys for wolverine (Magoun *et al.*, 2007; Gardner *et al.*, 2010) and North American river otters *Lontra canadensis* (Aing *et al.*, 2011). These studies used temporal replication to estimate detection probabilities and occupancy rates.

Wary and elusive carnivores such as wolverine and Canadian lynx occur in rugged and remote landscapes and are rarely observed and difficult to monitor. Little is known about their population status and trends throughout much of their range. Wolverine populations are thought to be threatened by trapping (Krebs *et al.*, 2004), declining snow packs (Brodie & Post, 2010; Copeland *et al.*, 2010; McKelvey *et al.*, 2011), back-country recreation (Krebs, Lofroth & Parfitt, 2007), industrial development (Krebs *et al.*, 2007) and potentially competition with other large carnivores (Inman *et al.*, 2012). Consequently, they have been designated as *Warranted for Protection* under the US Endangered Species Act (Inman *et al.*, 2012) and *Special Concern* (Committee on the Status of Endangered Wildlife in Canada (COSEWIC), 2003) in Canada. Canadian lynx populations are strongly dependent upon snowshoe hare *Lepus americanus* densities (Boutin *et al.*, 1995; O'Donoghue *et al.*, 1997; Krebs *et al.*, 2001). Lynx densities are lower along the southern portion of their range because of lower snowshoe hare densities (Murray, Steury & Roth, 2008) and anthropogenic habitat fragmentation (Koehler *et al.*, 2008; Murray *et al.*, 2008). Lynx are now listed as *Threatened* in the US (US Fish and Wildlife Service 2000),

and while are classified as *Not at Risk* in Canada, there is similar concern over viability of southern populations (Committee on the Status of Endangered Wildlife in Canada (COSEWIC), 2001). Development of inexpensive and non-invasive techniques is required to better understand the distribution and population trends of these species.

Here, we combine both spatial and temporal replication for snow surveys of large mammals throughout Banff National Park, Canada. While wolverine and lynx were focal species for this study, we simultaneously surveyed for cougar *Puma concolor*, coyote *Canis latrans*, deer *Odocoileus* spp. and moose *Alces alces*, all of which are difficult to census in rugged and forested landscapes. Survey routes ranged from 1- to 9-day back-country ski surveys. We developed four occupancy models that incorporated spatial correlation in detection probability and hierarchically estimated occupancy at two spatial scales: cell occupancy and segment presence. We conducted inference with both maximum likelihood (ML) and Bayesian Markov chain Monte Carlo (MCMC) methods for each model. We then assessed how trade-offs between spatial and temporal replication affect statistical power to detect changes in occupancy.

Study area

Our study area included 3900 km² of Banff National Park, Alberta, Canada (51.2 N, 115.5 W). The region contains rugged mountain topography (elevations range: 1000–3500 m) on the eastern side of the Continental Divide. The area receives long cold winters and short summers (Holland *et al.*, 1983). Deep snow depths in alpine areas near the Continental Divide taper to shallow snow depths in the Montane valley bottoms along the eastern edge of the park. Forests are dominated by Engelmann spruce *Picea engelmannii* and subalpine fir *Abies lasiocarpa* in the subalpine and lodge-pole pine *Pinus contorta* in the Montane. Carnivores in the region included wolverine, lynx, cougar, red fox *Vulpes vulpes*, coyote, wolf *Canis lupus*, black bear *Ursus americanus* and grizzly bear *Ursus arctos*. Ungulates in the region included elk *Cervus canadensis*, moose, mule deer *Odocoileus hemionus*, white-tailed deer *Odocoileus virginianus*, bighorn sheep *Ovis canadensis* and mountain goat *Oreamnos americanus*.

Methods

Snow-tracking occupancy surveys

We developed ski survey routes to sample thirty-nine 100-km² hexagons throughout Banff National Park during 2012 (Fig. 1). We divided each ski route into 1-km segments and conducted surveys from February through early April when snow consolidation provided easier and safer skiing conditions through avalanche terrain. For each 1-km segment, surveyors recorded the presence/absence of each species.

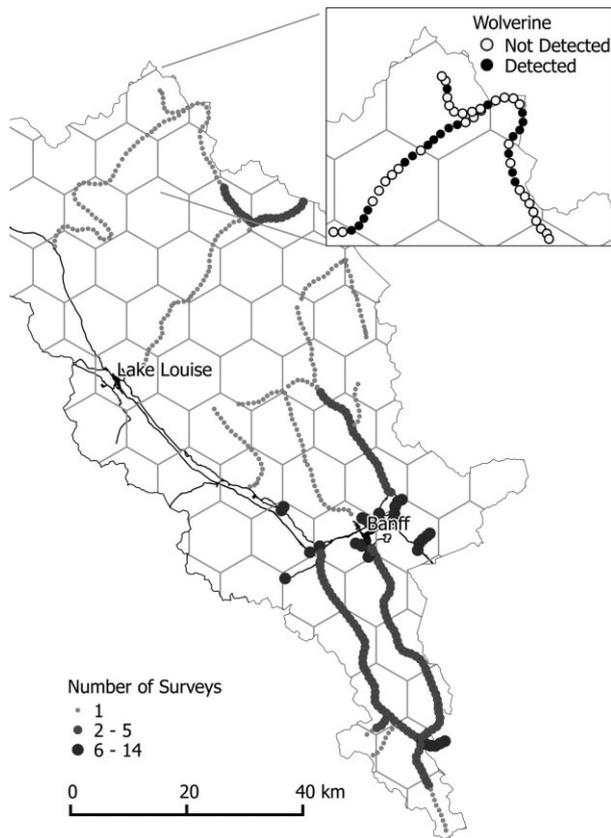


Figure 1 Map showing the number of times each 1-km segment was surveyed for wildlife tracks during 2012 in Banff National Park. Spatial and temporal replicates within the 100-km² hexagons were used to estimate detection probabilities. Each dot represents a 1-km long segment. The inset map shows a sequence of wolverine detections for a portion of the study area.

Surveyors estimated the maximum number of days that tracks could have persisted given previous snowfall, wind and sun events on each segment (DaysSnow) because we expected that this sampling window would influence detection rates. We recorded separate estimates of DaysSnow for carnivores and ungulates because ungulates penetrate deeper into the snow. We centred DaysSnow around the mean (3.7 for carnivores; 6.6 for ungulates) and divided by the standard deviation. We chose 100 km² as our grid cell size because it has been used to monitor wolverine in Ontario (Magoun *et al.*, 2007). Ellis, Ivan and Schwartz (2014) found that cell sizes of 100 and 225 km² had similar power to detect changes in wolverine density but that power decreased with larger cell sizes of 1000 km². While 100 km² might be the optimal cell size for wolverine, it may not be best for other species in our study with smaller home ranges.

Occupancy modelling

We developed four occupancy models that used both spatial and temporal replication to estimate occupancy rates. Data

considered are detection events y_{ijk} on cell i , the 1-km segment j and temporal replicate k . All models included parameters for occupancy ψ and detection probability p . Cell occupancy was a Bernoulli trial with a success parameter ψ , which can be interpreted as the proportion of study area occupied. We assumed that cell occupancy was independent of other cells and did not change during our surveys. We estimated ψ using the logit-linear function $\text{logit}(\psi) = \beta_\psi$ to constrain parameter estimates between 0 and 1. Detection probability p_i was the probability of detecting a species in cell i given that the cell was occupied. All of our models build upon these parameters and the general occupancy modelling approach of MacKenzie *et al.* (2002) who used a zero-inflated binomial model with the likelihood,

$$L(y | \psi, p) = \prod_{i=1}^M \{ \text{Bin}(y_i | K, p) \psi + I(d_i = 0)(1 - \psi) \}$$

Here, M is the number of cells surveyed, K is the number of times each cell is surveyed, y_i is the number of times the species was detected out of K surveys and d_i is the total number of detections in cell i . $I(\cdot)$ takes the value 1 when the expression in the brackets is true and 0 otherwise. The first term in the likelihood expression describes detection at the occupied sites using a binomial model. The second term describes sites where the species was never detected and the species may be truly absent.

Our first model, which we term Independent Detection, assumes the spatial and temporal replicates are independent and exchangeable. The likelihood for this model can be calculated as

$$L(y | \psi, p) = i = 1M \left\{ \left(\prod_{j=1}^{J_i} \prod_{k=1}^{K_{ij}} p_{ijk}^{y_{ijk}} (1 - p_{ijk})^{1 - y_{ijk}} \right) \psi + I(d_i = 0)(1 - \psi) \right\}$$

where $\text{logit}(p_{ijk}) = \alpha_{\text{Intercept}} + \alpha_{\text{DaysSnow}} \text{DaysSnow}_{ijk}$.

Our second model, which we term Markovian Detection, follows the same structure as the Independent Detection model, except that detection probabilities are autoregressive in space. It is based upon the spatially replicated models of Hines *et al.* (2010) where the probability of detection is affected by detection on the previous segment during the same sampling occasion. Thus,

$$\text{logit}(p_{ijk}) = \alpha_{\text{Intercept}} + \alpha_{\text{y}_{i,j-1,k}} y_{i,j-1,k} + \alpha_{\text{DaysSnow}} \text{DaysSnow}_{ijk}$$

The first segment of a survey lacks a previous segment and thus y_{j-1} could be either 0 or 1. Therefore, we used a weighted mean detection probability p_{mean} for the first segment. We calculated both p and p' for y_{j-1} equal to 0 and 1 respectively and then calculated $p_{\text{mean}} = \frac{p}{p + (1 - p')}$ (Hines *et al.*, 2010).

Our third and fourth models hierarchically modelled occupancy at two spatial scales: cell occupancy and segment presence (Nichols *et al.*, 2008), and therefore, segment presence is conditional on the cell being occupied, and detection at a segment conditional on presence at the segment. Our third model, which we term Independent Segment, assumes that if a cell is occupied, segments have a probability of species presence θ . Probability of presence on one segment does not influence probability of presence on other segments. Note that a species could be present but not detected on a segment, and that if the cell is unoccupied, all segments are also unoccupied. Moreover, the probability of species presence on a segment is the product $\psi\theta$ and detection probability p is probability of detection given the segment is occupied. Multiple surveys of segments at different points in time are used to estimate detection probability. We modelled θ in a logit-linear form such that $\text{logit}(\theta) = \beta_\theta$. We nested temporal replicates within spatial replicates similar to Mordecai *et al.* (2011). The likelihood for this model is

$$L(y | \psi, p, \theta) = \prod_{i=1}^M \left\{ \prod_{j=1}^{J_i} \left(\prod_{k=1}^{K_{ij}} p_{ijk}^{y_{ijk}} (1 - p_{ijk})^{1 - y_{ijk}} \right) \theta + I(d_{ij} = 0)(1 - \theta) \right\} \psi + I(d_i = 0)(1 - \psi)$$

Our fourth model, which we term Markovian Segment, is similar to the Independent Segment model except that probability of species presence on a segment is autoregressive in space. Species presence on one segment depends upon species presence on the previous segment. We thus calculated θ as $\text{logit}(\theta_{ij}) = \beta_\theta + \beta_{\text{lag}} \Phi_{ij-1}$. Here, Φ is a latent variable for whether or not the species was present on the previous segment. This model is similar to the Hines *et al.* (2010) first-order Markovian process model, except it contains within segment temporal replication. For the first segment of each cell where the state of the previous segment is unknown, we used a weighted average of θ (as above) for $\Phi_{j-1} = 0$ and 1, respectively.

We estimated parameters for all models using both MCMC and ML approaches. ML approaches were preferable for model comparisons and power analyses (see below), but we also provided MCMC methods because they can be more easily extended into multi-season occupancy models. For each ML model, we estimated all parameters on the logit scale using the optim function in R and the quasi-Newton algorithm for optimization. For each MCMC model, we estimated ψ on the probability scale with a Uniform(0, 1) prior distribution and all other parameters on the logit scale using a Normal(0, 100) prior distribution. We ran three chains with randomly generated starting values and 60 000 iterations per chain. We removed the first 10 000 iterations (burn in) and then selected every fifth iteration for analysis. We assessed MCMC convergence by examining trace plots and the Gelman–Rubin statistic where values <1.1 suggest no evidence for lack of convergence (Kéry & Schaub, 2011).

Power analyses

We assessed the trade-offs between spatial and temporal replication in occupancy surveys by conducting statistical power analyses. We examined how the distribution of spatial and temporal replicates, spatial correlation in detection probability and number of cells (50 and 100) affected power to detect absolute decreases in occupancy ranging from 0 to 0.5 over a single time interval. We used 16 total replicates, which was lower than our mean number of replicates per cell (22). We used three combinations of spatial and temporal replicates: 1 spatial and 16 temporal; 4 spatial and 4 temporal; and 16 spatial and 1 temporal. We used two mean detection probabilities (0.15 and 0.30) and two levels of serial correlation in detection probability. Those levels of serial correlation were independence ($p = p'$) and strong serial correlation ($p' - p = 0.6$). We calculated power by data simulation. For each simulation, we created two independent data sets, the first with $\psi = 0.75$ and the second with ψ ranging between 0.25 and 0.75. For simulations with spatial replication, we applied our Markovian Detection ML model to the two data sets; otherwise, we applied our Independent Detection model. We calculated occupancy and standard errors for each data set on the probability scale using the delta method. We then calculated a Wald statistic as $\frac{|\hat{\psi}_1 - \hat{\psi}_2|}{\sqrt{(\widehat{SE}_{\psi_1}^2 + \widehat{SE}_{\psi_2}^2)}}$ (Guillera-Aroita & Lahoz-Monfort,

2012). We ran 1000 simulations per scenario and calculated power as the percentage of simulations with a Wald statistic greater than 1.96 (two-sided type I error = 0.05). For the first segment of each survey, we used the weighted mean detection probability in data simulation and analysis. We compared our power estimates to baseline power with $p = p' = 1$. For these perfect detection probability scenarios, we generated occupancy data with no replicates, estimated parameters using standard logistic regression and calculated a Wald statistic as above.

We performed our analyses using R 3.0.2 (R Development Core Team, 2013), an R interface to JAGS 3.3 (<http://sourceforge.net/projects/mcmc-jags>) and QGIS 1.8 (www.qgis.org). All data and R-scripts for occupancy modelling and power analysis can be found in Supporting Information Appendix S1–S4. Data are also available from the Dryad Digital Repository: <http://doi.org/10.5061/dryad.v4p20>.

Results

We accumulated 872 km of snow-tracking surveys across 39 cells. Each cell contains an average of 11.7 segments (median = 11, range = 2–27). We conducted multiple surveys on 44% of the cells and 40% of the 443 segments. We detected each species on between 6 (cougar) and 23 (wolverine) of the 39 cells.

Occupancy estimates from the MCMC Markovian Detection model were highest for wolverine, lynx and moose and lowest for cougar (Fig. 2). Within each species, occupancy estimates for the Independent Detection and Independent Segment models were similar. Occupancy estimates

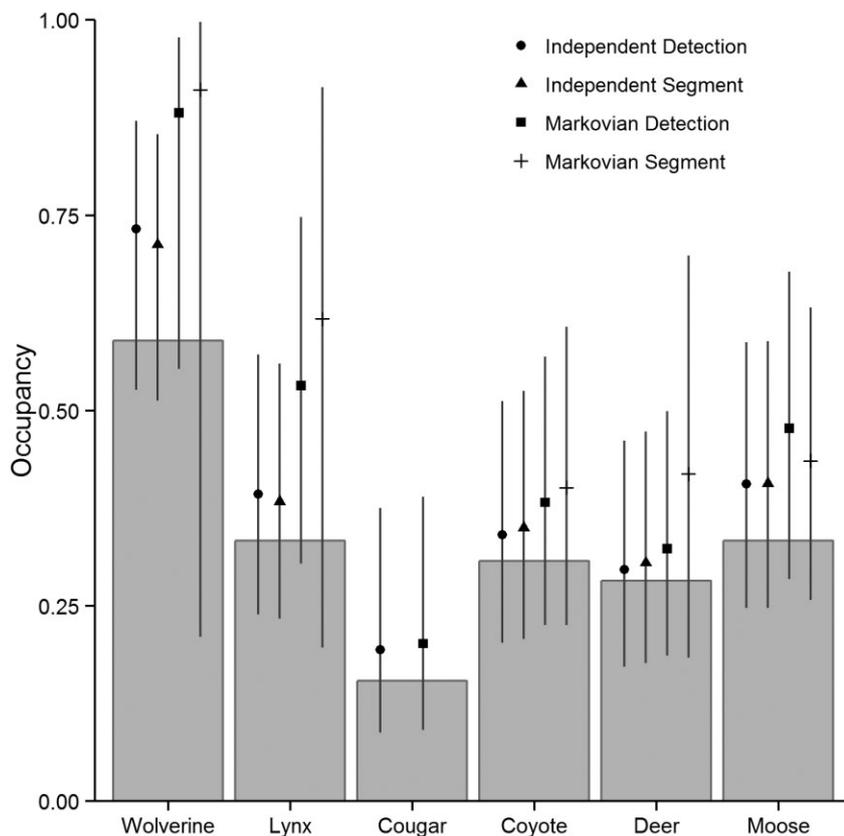


Figure 2 Proportion of cells where each species was detected (shaded bars) and predicted occupancy rates (black points with 95% confidence intervals) for each maximum likelihood model. Thirty-nine hexagons were sampled in 2012.

were slightly higher for the two Markovian models than the two Independent models. The Markovian Segment models had the highest occupancy estimates but also had the largest confidence intervals.

The Markovian Detection model had the lowest Akaike information criterion (AIC) for all species (Fig. 3). We removed the cougar Independent and Markovian models because of wide confidence intervals (CIs) and periodicity in MCMC trace plots. The Markovian Detection lag term for whether or not the species was detected on the previous segment was significantly greater than zero for all species, which suggests strong serial correlation in detection probabilities at the 1-km segment scale (Fig. 4). Weighted mean detection probabilities at the mean DaysSnow were as follows: wolverine 0.12, lynx 0.16, cougar 0.14, coyote 0.31, deer 0.45 and moose 0.15. Detection probability significantly increased with DaysSnow for wolverine and moose but not for other species. ML and MCMC methods produced similar parameter estimates.

Our power analysis found that temporal and spatial replicates have the same power to detect decreases in occupancy when segments are independent (Fig. 5). Temporal replicates have higher power than spatial replicates when segments are spatially correlated. Increasing mean detection probability and number of cells sampled reduced the difference in power between spatial and temporal replicates. Given our choice of survey effort and detection probability,

power for temporal replicates and independent spatial replicates was equal to or slightly below our baseline power of perfect detection.

Discussion

Recent advances in occupancy modelling techniques have made track surveys with spatial replication increasingly promising approach for monitoring wide-ranging species over large geographical areas (Hines *et al.*, 2010; Guillera-Aroita *et al.*, 2011; Thorn *et al.*, 2011). The addition of temporal replicates to spatial replicates increases the cumulative probability of detection and thus improves precision of occupancy estimates. Like Hines *et al.* (2010), we found that modelling spatial correlation between adjacent trail segments increased occupancy estimates and failing to account for the spatial correlation would result in negatively biased occupancy estimates with increased type I error associated with narrow CIs. Given the prevalence of winter snow-based tracking studies in monitoring (Stephens *et al.*, 2006; Golden *et al.*, 2007; Linnell *et al.*, 2007; Magoun *et al.*, 2007; Gardner *et al.*, 2010; Aing *et al.*, 2011; Webb & Merrill, 2012), spatially and temporally replicated occupancy surveys are a promising monitoring technique.

We chose to split transects into 1-km segments and model spatial correlation among segments using Markovian processes as described by Hines *et al.* (2010). Other

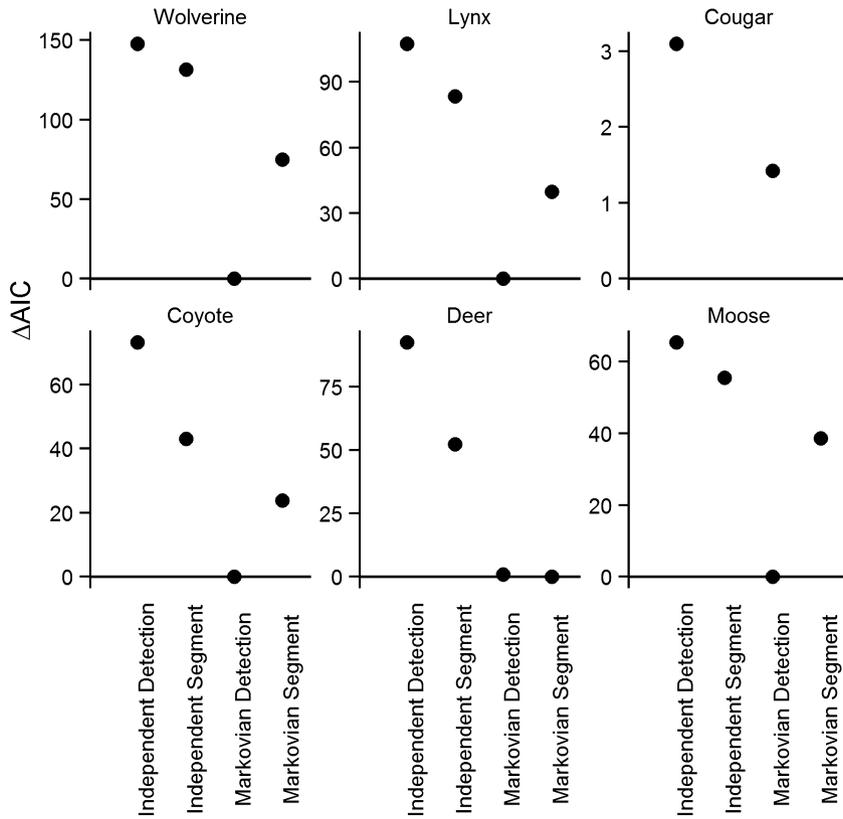


Figure 3 Comparison of ΔAIC (Akaike information criterion) values from maximum likelihood models where ΔAIC equals AIC minus the model with the minimum AIC . The most parsimonious model for each species has a ΔAIC value of 0.

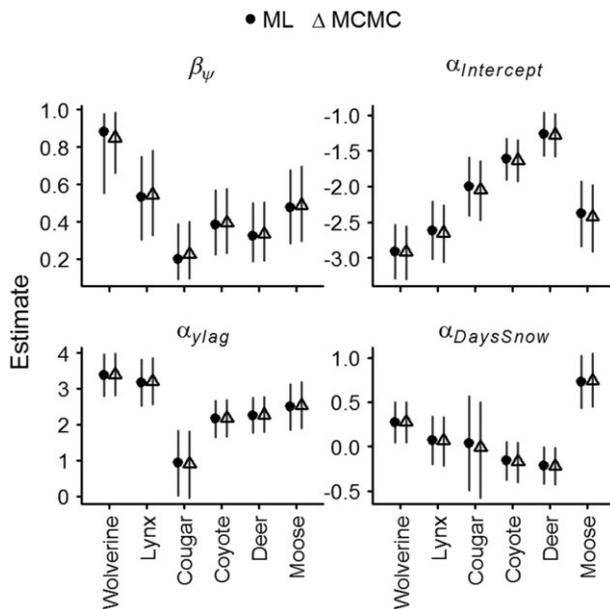


Figure 4 Parameter estimates and 95% confidence intervals [maximum likelihood (ML)] and 95% credible intervals [Markov chain Monte Carlo (MCMC)] for each species.

approaches for dealing with spatial correlation include increasing segment size until segments show no spatial correlation (Thorn *et al.*, 2011), using autoregressive models (Aing *et al.*, 2011; Burton *et al.*, 2012), including transect

level random effects in state-space models (Mordecai *et al.*, 2011), and using Markov-modulated Poisson processes to model clustered species detections (Guillera-Arroita, 2011; Guillera-Arroita *et al.*, 2012). The advantage of this later approach is that transects do not need to be split into discrete segments. We chose a Markovian approach with discrete segments because it was intuitively simple and we could model movement processes for species travelling long distances on trails.

Our analysis did not include habitat- or human use-related covariates that could affect probability of detection, cell occupancy, or colonization and extinction rates (Kéry, Guillera-Arroita & Lahoz-Monfort, 2013). Inclusion of larger scale, cell-level explanatory variables such as spring snow cover for wolverine (Copeland *et al.*, 2010; McKelvey *et al.*, 2011) and indices of hare abundance for lynx (Boutin *et al.*, 1995; O'Donoghue *et al.*, 1997; Krebs *et al.*, 2001) could be important for understanding the mechanisms behind changes in species occupancy (Mattfeldt, Bailey & Grant, 2009). Moreover, including covariates at both the cell and the segment scales can be important for understanding how processes operating at multiple spatial scales affect species occurrence (Mordecai *et al.*, 2011; DeCesare *et al.*, 2012).

We found that while spatial and temporal replicates have identical statistical power to detect changes in occupancy with independent segments, spatial correlation in detection probability reduced power. The negative effects of spatial correlation decreased with increased detection probability

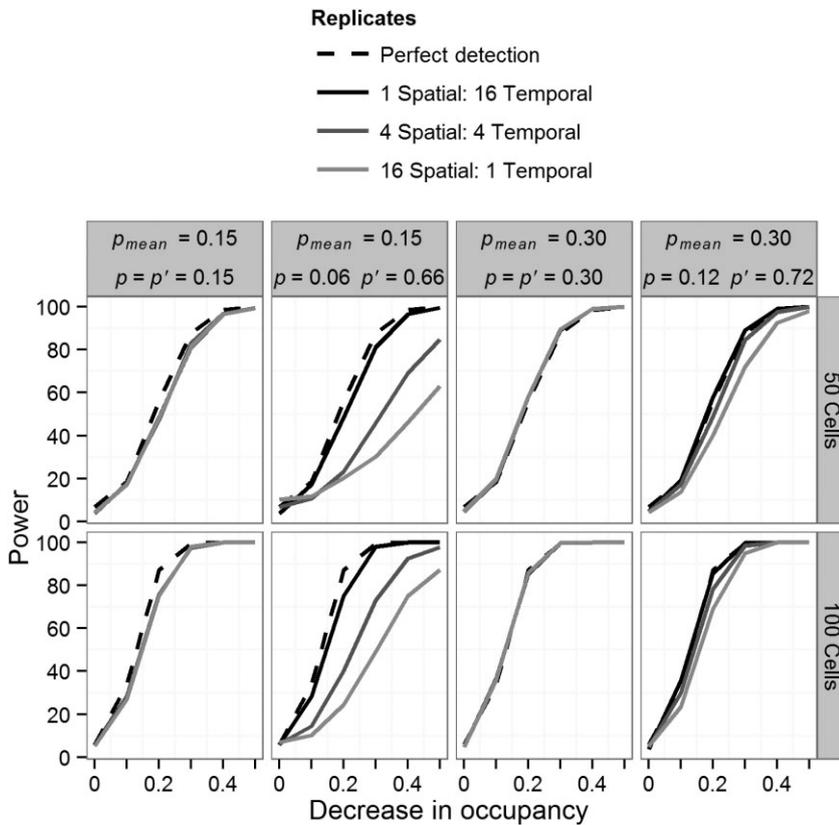


Figure 5 Statistical power to detect decreases in occupancy. Simulations examined how mean detection probability, levels of serial autocorrelation and number of cells (50 and 100) affected power using spatial and temporal replicates. Segments were independent for simulations with $p = p'$, where p and p' indicate detection probabilities for when the species was not and was detected on the previous segment, respectively. Segments had strong serial correlation for simulations with $p' - p = 0.6$. Power analyses were conducted with a starting occupancy probability of 0.75 and absolute decreases in occupancy ranging from 0 to 0.5. Simulations tested for significant changes in occupancy using a Wald test with a two-sided type I error of 0.05.

and number of sites sampled. Power to detect small changes in occupancy was constrained by the number of cells rather than the number of replicates. Thus, approximately 100 cells are required to achieve 80% power to detect a 0.2 decrease in occupancy over a single time period. If managers were interested in the number of cells occupied rather than ψ , then finite population corrections could potentially be applied to reduce variance and increase power (Ellis *et al.*, 2014). If managers were interested in longer term trend estimates rather than short-term changes in occupancy, increasing the number of seasons sampled would reduce variance around the trend estimate and would thus increase power (MacKenzie, 2005). Decisions on how to allocate effort towards number of sites and spatial versus temporal replicates are an important component of robust study design (MacKenzie & Royle, 2005; Bailey *et al.*, 2007; Guillera-Arroita, Ridout & Morgan, 2010; Guillera-Arroita & Lahoz-Monfort, 2012) and will depend upon spatial correlation in detection probability, mean detection probability and costs required to access sites.

In our study, wolverine and lynx had the highest level of spatial correlation and relatively low detection probabilities. Thus, future surveys require more than 16 replicates per cell and an expanded study area. Inclusion of habitat-related covariates at the cell and segment spatial scales could improve estimates of cell occupancy, segment presence and detection probability which would increase power to detect spatial variation in occupancy. Interestingly, Ellis *et al.*

(2014) found through simulation that most temporally replicated occupancy sampling schemes for wolverine snow surveys had low power to detect decreases in occupancy associated with declines in density. Their low power was likely driven by spatial overlap of wolverine home ranges (Gaston *et al.*, 2000; Stanley & Royle, 2005). Wolverine in these simulations could travel large distances across cells and thus the movements of a few individuals could mask declines in density. We directly examined power to detect changes in occupancy rather than density and our results are especially applicable to situations where changes in occupancy are driven by changing habitat quality, climatic conditions and human activity.

Our estimates of occupancy can provide managers with useful indices for estimating the abundance and distribution of difficult to monitor threatened species. For example, adult female wolverine home ranges along the Rocky Mountains range from an average of 139 km² in Glacier National Park Ecosystem (Copeland *et al.*, 2010) to 303 km² in the Yellowstone Ecosystem (Inman *et al.*, 2012). Wolverine occupied approximately 3300 km² of our study area. Given these home-range sizes, <2% overlap between same sex adults (Inman *et al.*, 2012), and assuming females occurred in all cells, between 10 and 23 adult female wolverines likely used our study area. Adult female lynx in the Southern Canadian Rockies had average 100% minimum convex polygon home ranges of 211 km² (Apps, 2003) and same sex overlap for lynx can be very high (Poole, 1995).

Given that lynx occupied approximately 2100 km² of our study area, our study area likely contained a minimum of 10 adult females. These population estimates are approximate and have inherent limitations. For example, if wolverine and lynx use portions of the 100-km² grid cells because their home range straddles two cells, then we would overestimate the area occupied and the minimum number of animals. However, if that were the case, we would expect low values of θ for our hierarchical segment models. Conversely, we would underestimate the minimum number of individuals for species whose home ranges overlap. The next step is to understand how changes in population size affect the amount of home-range overlap and occupancy–abundance relationships (Gaston *et al.*, 2000; Tempel & Gutiérrez, 2013).

We used a hierarchical approach to combine spatial replication across the study area with temporal replication for portions of the study area to estimate detection probabilities and occupancy. The advantage of applying temporal replication to spatial surveys is it increases precision in estimates of occupancy and detection probability and it can reduce biases in occupancy estimators. Ground snow-tracking surveys are a potentially powerful tool because they simultaneously monitor multiple species over large spatial areas. Our approach to analysing snow-tracking surveys could be applied to other study areas looking to monitor species of conservation concern such as wolverine and lynx across remote and rugged landscapes.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Comparison of all ML and MCMC parameter estimates.

Table S1. Banff_2012.csv includes all data used for this analysis.

Appendix S1. Occupancy Maximum Likelihood.R.

Appendix S2. Occupancy MCMC.R.

Appendix S3. Plot Results.R.

Appendix S4. Power Analysis.R.